Algological Studies **71**	81–102	Stuttgart, November 1993

Soil algae in four secondary successional stages on abandoned fields

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With 4 figures and 6 tables in the text

Abstract: Communities of soil algae (species composition, counts, spatial distribution, temporal changes) were studied in relation to secondary succession on abandoned fields on cambisol, namely in intensively cultivated field, in for 2–10 years uncultivated fields (fallow, and meadow, respectively) and in an oak forest. In total, 121 algal species (more than 30 were new for the Czech Republic) were found during a two-year investigation.

Members of the Chlorophyceae dominated in the area, their proportion in the algal community increased with the age of successional stage. The greatest algal species diversity was recorded in the meadow (99 species), followed by the fallow (90), the field (85) and the forest (49). The most similar algal communities were in the field - fallow ($S_s = 0.8914$) and in the fallow - meadow ($S_s = 0.8783$), the least similar on the other hand in the field - forest ($S_s = 0.4776$). The highest mean abundance of algal cells in the 0–10 cm soil layer was found in the fallow and in the field (62.10^9 and $60.10^9 \cdot m^{-2}$, respectively) and decreased to the meadow ($31 \cdot 10^9 \cdot m^{-2}$) and the forest ($0.15 \cdot 10^9 \cdot m^{-2}$). With soil depth, algal counts decreased more significantly than numbers of species. Both heterogeneity and temporal changes of algal communities were most distinct in the forest and the field, Bacillariophyceae and Cyanophyceae varied more than Chlorophyceae together with Xanthophyceae and Eustigmatophyceae.

Key words: Soil algae, secondary succession, abandoned field, algal diversity, algal counts, Chlorophyceae, Xanthophyceae, Bacillariophyceae, Cyanophyceae, cambisol.

Introduction

Microscopic algae are a common component of all terrestrial ecosystems. Their important role as primary producers and nitrogen fixers, as well as their ability to improve soil structure, is generally known (HOLLERBACH & ŠTINA 1969, METTING 1981).

The function of algae in each soil biotope is closely related to the structure of corresponding algal community; the comparable data of soil algal communities of various ecosystems are therefore desirable for predicting their role in given

0342-1120/93/0100-0081 $ 5.50

conditions. The character of algal flora of each locality is a result of a complex influence of the local vegetation type, soil properties and climatic conditions (HOLLERBACH & ŠTINA 1969, ŠTINA & HOLLERBACH 1976, METTING 1981, NAKANO 1981, STARKS et al. 1981, ALEKSACHINA & ŠTINA 1984), but often depends also on the input of algal diaspores from air (BROWN et al. 1964). The determination of the main ecological factors affecting the character of local soil algal community is often difficult. One of the suitable ways for their discovery seems to be the investigation of algae in different ecosystems situated in one and the same soil type and climatic area, best in relation to the succession processes.

The changes of soil algal flora in relation to the primary succession were studied several times, particularly in special ecological situations, e. g., algal colonization on postvolcanic substrates (SCHWABE 1972, BROCK 1973, CARSON & BROWN 1978, RAYBURN et al. 1982, etc.), and on new substrates arisen from human activity (TARČEVSKIJ & ŠTINA 1967, ŠUŠUJEVA 1977, 1985, STARKS & SHUBERT 1979, 1982, LUKEŠOVÁ & KOMÁREK 1987). On the contrary, the knowledge of the changes in algal communities features connected with the secondary succession is poor (HUNT et al. 1979).

The aim of this study was to identify and quantify soil algae of four secondary successional stages (field, fallow, meadow, forest) of a cambisol in South Bohemia (Czech Republic). The study was part of a complex ecosystem research project realized by Institute of Soil Biology, Academy of Sciences of the Czech Republic, České Budějovice.

Material and methods

Site description

The soils of following localities representing four secondary successional stages were studied:

Field – stage 1: intensively cultivated field with wheat in 1986 (NPK – 210 kg · ha^{-1}, Basagran and Aminex at dose 2+2 kg · ha^{-1}), potatoes in 1987 (farmyard manure – 5000 kg · ha^{-1}), barley in 1988 (NPK – 210 kg · ha^{-1}). The site was almost weedless.

Fallow – stage 2: abandoned field 1–3 years old, *Apera spica venti, Plantago uliginosa, Tripleurospermum inodorum, Spergula arvensis* and *Raphanus raphanistrum* dominated in the early phase of the succession (year 1986); *Sagina procumbens, Tripleurospermum inodorum, Vicia hirsuta, Agrostis gigantea* and *Epilobium adenocaulon* prevailed in the second year and *Agrostis tenuis, Agropyron repens, Cirsium arvense* and *Epilobium adenocaulon* in the third year.

Meadow – stage 3: field uncultivated for 8–10 years, but mown up to 1985 year. Dominant vascular plant species were *Holcus lanatus, Holcus mollis, Prunella vulgaris, Lathyrus pratensis.*

F o r e s t – stage 4: 60–70 years old subclimax, acidophilous oak wood, dominated by *Quercus robus,* and containing limited numbers of *Picea abies, Tilia cordata, Fraxinus exelcior, Acer pseudoplatanus* and *Fagus sylvatica.*

All stages were situated in South Bohemia, stage 1–3 near the village of Dlouhá Ves (49° 06′ N, 14° 07′ E, 570 m above see level), stage 4 near the village of Malovice-Hradiště (49° 04′ N, 14° 09′ E, 480 m above see level).

This area is characterized by a mean annual precipitation of 605 mm (405 mm in the vegetation period), a mean annual temperature of 7.3 °C (13.2 °C in the vegetation period) (collective farm "Mír"Chelčice meteorological station), by migmatized paragneis prevailing in the bedrock and by cambisol soil type. Stages 1 and 2 had an arable humus horizon, stages 3 and 4 a mull horizon and a mull-moder horizon respectively. Detailed characteristics of studied localities are given in Table 1.

Table 1. Some physical and chemical soil properties, and plant biomass measured in the period of maximum development of vegetation. Mean values ($\bar{x}$) and coefficients of variation (V [%]) are given.

	Soil depth [cm]	Field		Fallow		Meadow		Forest	
		$\bar{x}$	V [%]	$\bar{x}$	V [%]	$\bar{x}$	V [%]	$\bar{x}$	V [%]
Moisture[a] [%]	L	–		–		–		54.0	24
	0–1	19.0	26	18.4	23	27.8	13	26.6	13
	1–10	16.6	11	15.5	16	22.7	20	16.4	25
Temperature [°C]	5	7.5	81	8.2	76	7.8	75	7.8	64
pH [H_2O][b]	0–10	5.8		6.0		5.3		5.2[c]	(4.6)[d]
C org. [%][b]	0–10	1.5		1.2		2.2		4.8	(2.4)
N tot [%][b]	0–10	0.13		0.12		0.24		0.95	(0.22)
P tot [%][e]	0–10	0.095		0.086		0.079		0.090	(0.060)
C/N	0–10	11.2		10.0		9.2		5.7	(10.9)
	year								
Aboveground plant biomass dry matter [$g \cdot m^{-2}$]*	1986	1276.6		285.8		434.6		54.4	
	1987	–		521.2		627.5		86.4	
Underground plant biomass dry matter, 0–10 cm [$g \cdot m^{-2}$]*	1986	321.0		–		1470.0		457.0	
	1987	–		167.0		1207.0		899.0	

a: in field, fallow and meadow measured in layers of 0–1, 1–10 cm, in forest in horizons L (litter), A, B
b: data overtaken from Šantrůčková & Straškraba (1991)
c: horizon A
d: horizon B
e: according to Kalčík (pers. comm.)
*: according to Matějka (pers. comm.).

Five experimental plots (quadrats 2.5 × 2.5 m), selected at random out of 60 marked out at each successional stage, were used for the investigation of soil algae.

Sampling

Species composition and counts of algae were studied monthly during the period of April 1986 - January 1988 at each of the 4 stages, complementary characteristics, such as, for example, vertical distribution, still over years 1988–1989. Soil samples were taken aseptically from two layers (0–1 and 1–10 cm) in the field, the fallow and the meadow, and from litter, A horizon and B horizon to the depth of 10 cm in the forest, using metal sampling corer with a working area of 10 cm^2. Fresh soil samples composed of 5 subsamples (each subsample from one of the 5 plots) mixed together were analysed. For the study of the horizontal algae distribution (heterogeneity, respectively) individual subsamples were analysed separately. For the detailed study of the vertical distribution of algae (made once per study period) soil samples were taken from the depth of 0–2, 10–12, 20–22, 25–26 (bedrock), 30–32, 40–42, 50–52 cm.

On each sampling occasion, soil moisture was determined gravimetrically as the percentage of the wet weight, and soil temperature was measured in the depth of 5 cm.

Algal counts (numbers)

Dulution method on solid media was chosen for algae enumeration because low algal numbers in the forest made it impossible to use direct counting methods (algae cells were not detectable even under fluorescence microscope). A high proportion of protonemata of mosses in studied soils unenabled also the use of chlorophyll extraction for algal biomass determination.

Ten grams of soil were homogenized ultrasonically in 90 ml sterile water for 4 minutes and serial 4-fold dilutions of homogenate in liquid BOLD's Basal Medium (BBM) (BISCHOFF & BOLD 1963) were prepared. Each Petri dish containing BBM, the suitability of which for all algal groups was verified experimentally, solidified with 1.5 % agar, was inoculated with 1 ml of diluted soil suspension; 4 replications of each dilution were used. Incubation proceeded at laboratory temperature (20 ± 2°C) under a 12 h photoperiod (5.5 W · m^{-2}).

Numbers of algae were estimated by counting algal colonies developed on agar plates of the most suitable dilution (20–400 colonies per plate), supposing 1 cell = 1 colony. Colonies of Chlorophyceae* (CH), Xanthophyceae (X) and Eustigmatophyceae (E) (further in the text CH + X + E) were counted together because of the difficulty to distinguish them. Bacillariophyceae (B) and CH + X + E were counted after 3 weeks and Cyanophyceae (C) after 5 weeks of incubation. Numbers of algae (colonies, in fact) were related to 1 g dry weight (d. w.) of soil or converted to 1 m^2 using data on bulk density.

Species composition

Two procedures were used parallely for the identification of algae. The first one was the same as for quantitative purposes. After counting, algal colonies were examined microscopically. Only few algal species could be identified directly this way, the majority of algal strains had to be isolated into unialgal cultures and their life cycles studied for correct species identification.

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* Chlorophyceae s. l. (Chlorophyta resp.) in the old sense were used for simplicity. Today, Chlorophyta are divided into several classes (ETTL 1983, BOURRELLY 1988).

The second method was the modified "growth slides" method (LUND 1945). Soil samples were placed into sterile Petri dishes, covered with sterile coverglasses, moistened with sterile water and incubated at laboratory conditions (20 ± 2°C, day light). Coverslips were removed and actively growing algae adhering to them were examined microscopically 3 times at fortnight intervals and subsequently 3 months later from the beginning of incubation. Both methods used were enlarged by direct microscopic observation both of top soil layer and of slides burried in (PIPE & CULLIMORE 1980) or arranged on the surface of soil in field conditions.

Permanent preparations of diatoms made by means of hot cleaning of frustules in 30 % H_2O_2 and mounting in pleurax medium facilitated a correct species identification of this group.

Evaluation of data obtained

Floristic similarity of soil algal communities was estimated by means of SORENSEN's coefficient of similarity (S_s) measuring the ratio of common species number to the total number of species in compared stages.

Algal species found in 75 % of soil samples from all samples examined in each locality are supposed to be highly constant species.

The heterogeneity of species composition of algal community, made twice during the period of investigation, was stated by percentage proportion of lowly and highly frequent species from total numbers of isolated species. Species found in one or two plots from five examined at each stage are considered to be lowly frequent, species found in four or five plots are taken to be highly frequent.

Temporal fluctuation of algal counts as well as that of soil moisture, temperature and heterogeneity of algal numbers were characterized by means of coefficients of variation. Confident limits ($\alpha = 0.05$) were constructed to reveal significant differences in algal counts and species numbers of compared stages and soil layers respectively.

Agglomerative method "complete linkage" (cluster analysis) using SORENSEN's coefficient of similarity and based on the species presence and absence data was used as comparison of algal communities in studied successional stages.

The ordination of samples, characterized by species composition of algae, was accomplished by the method of DCA-detrended correspondence analysis (HILL & GAUCH 1980); the first two axes were used for depicting.

Results

Algal counts

The highest mean counts (abundance) of algae in the 0–10 cm layer were found in the fallow ($62.10^9 \cdot m^{-2}$) and decreased in the sequence field ($60.10^9 \cdot m^{-2}$), meadow ($31.10^9 \cdot m^{-2}$) and forest ($0.15 \cdot 10^9 \cdot m^{-2}$). The mean counts of CH + X + E represented 94–100 % of the total numbers of algae and their proportion increased

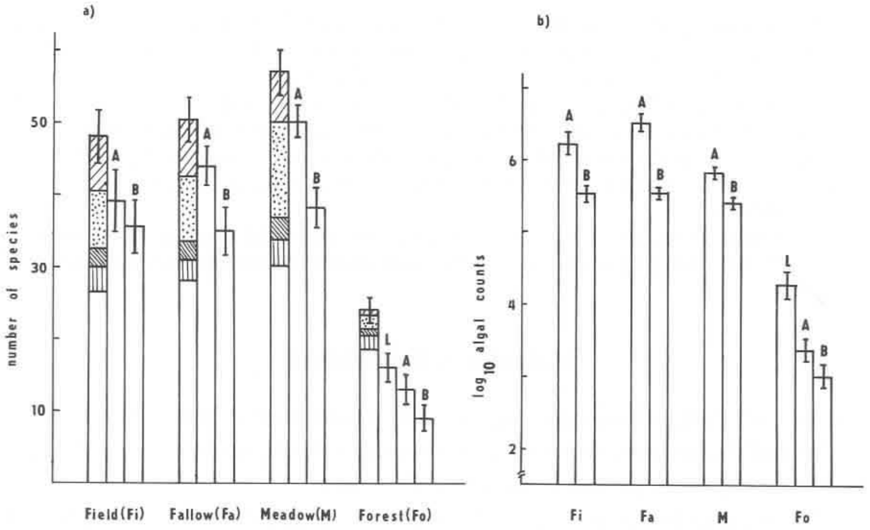

Fig. 1. Vertical stratification of algae. **a)** ... mean numbers of algal species, **b)** ... $\log_{10}$ of mean algal cell counts [$\cdot g^{-1}$ d. w. of soil], **A** ... 0–1 cm soil layer (in forest horizon A), **B** ... 1–10 cm soil layer (in forest horizon B), **L** ... litter.
▨ Cyanophyceae, ▢ Bacillariophyceae, ▧ Eustigmatophyceae, ▥ Xanthophyceae, □ Chlorophyceae. ⊢●⊣ confident intervals ($\alpha = 0.05$).

with the successional age of the locality. The proportion of Bacillariophyceae in total counts ranged between 0.42–3.03 %, maximum being in the field; the proportion of Cyanophyceae reached 2.97–4.66 %, with maximal value in the fallow.

The algal counts of all groups investigated in individual soil layers are given in Table 2. The statistically significant differences were found among algal numbers of all compared stages in the surface soil layer, but in deeper soil layer only between those of forest and younger stages (Fig. 1).

Species composition

In total, 121 algal species were recorded from studied localities during the two years' investigation (Tab. 3). More than 30 identified species were new for the flora of the Czech Republic, several others, for example *Lobosphaera* sp., *Chlorosarcinopsis* sp., *Spongiochloris* sp., do not coincide with the description of any known species. Chlorophyceae dominated both in quality and quantity in the area studied. Following species were found most regularly: *Stichococcus bacillaris, Tetracystis aggregata, Eustigmatos magnus, Klebsormidium flaccidum, Bracteacoccus minor, Nostoc calcicola, Coccomyxa gleobotrydiformis, Hantzschia amphioxys, Chlorella ellipsoidea* and *Pseudococcomyxa simplex.*

Table 2. Average x̄, maximum and minimum counts of algal cells · $10^3 \cdot g^{-1}$ d · w · of soil and coefficients of variation V [%].

		Field				Fallow				Meadow				Forest			
Group	Soil depth* [cm]	x̄	min	max	V [%]	x̄	min	max	V [%]	x̄	min	max	V [%]	x̄	min	max	V [%]
Cyano-	(L)	–	–	–	–	–	–	–	–	–	–	–	–	< 0.1**	–	–	–
phyceae	0–1 (A)	45.5	5.0	196.0	114	165.5	11.9	369.5	77	16.6	5.5	43.0	87	< 0.1	–	–	–
	1–10 (B)	9.5	1.0	34.4	102	7.8	2.4	17.2	65	8.9	2.7	24.7	72	< 0.1	–	–	–
	(L)	–	–	–	–	–	–	–	–	–	–	–	–	< 0.1	–	–	–
Bacillario-	0–1 (A)	64.8	10.9	246.9	104	32.3	9.7	249.5	160	5.3	1.2	16.5	71	< 0.1	–	–	–
phyceae	1–10 (B)	8.0	1.0	41.6	110	1.5	0.7	2.9	41	0.8	0.2	1.9	63	< 0.1	–	–	–
	(L)	–	–	–	–	–	–	–	–	–	–	–	–	19.4	2.4	94.8	126
CH + X	0–1 (A)	1554.4	261.0	5980.0	107	3044.1	1086.0	6753.0	59	663.9	249.0	1345.5	47	2.3	0.3	6.3	79
+ E***	1–10 (B)	311.3	44.4	812.6	56	186.1	78.7	342.1	36	247.3	115.0	543.3	52	0.8	0.1	1.9	80
	(L)	–	–	–	–	–	–	–	–	–	–	–	–	19.4	2.4	94.8	126
Σ	0–1 (A)	1664.7	295.5	6063.0	101	3241.9	1126.5	6959.0	55	685.8	265.4	1414.9	47	2.3	0.3	6.3	79
	1–10 (B)	328.9	53.7	826.0	54	195.5	95.9	356.6	35	256.9	119.0	556.6	51	0.8	0.1	1.9	80

* 0–1, 1–10 cm in field, fallow and meadow, horizon L litter, A and B to the depth of 10 cm in forest.
** Algal counts < $0.1 \cdot 10^3 \cdot g^{-1}$ d · w · of soil are not taken into account.
*** CH + X + E Chlorophyceae together with Xanthophyceae and Eustigmatophyceae.

Table 3. The list of algal species and their constance [%] in soils of secondary successional stages in the years 1986–1987.
Fi ... field, Fa ... fallow, M ... meadow, Fo ... forest.

	Fi	Fa	M	Fo
CYANOPHYCEAE				
Anabaena sp.	35	40	20	-
Cylindrospermum licheniforme (BORY) KÜTZ.	60	70	100	-
Leptolyngbya nostocorum (BORN.) ANAGN. et KOM.	100	100	75	-
Leptolyngbya sp.	10	-	25	-
Microchaete tenera THUR.	-	-	65	-
Nostoc calcicola BREB.	100	100	100	65
N. minutum DESMAZ.	75	95	100	-
N. muscorum AG.	5	10	70	-
Nostoc sp.	-	-	20	-
Phormidium autumnale (AG.) GOM.	95	90	90	5
Plectonema boryanum f. *hollerbachianum* ELENK.	70	70	-	-
P. edaphicum (ELENK.) VAULINA	75	90	10	-
Pseudanabaena sp.	30	20	-	-
Pseudophormidium sp.	50	15	20	-
Trichormus variabilis (KÜTZ.) KOM. et ANAGN.	20	20	40	-
BACILLARIOPHYCEAE				
Achnanthes minutissima KÜTZ.	-	-	-	10
Eunotia tenella (GRUN.) HUST.	-	-	60	-
Gomphonema angustatum (KÜTZ.) RABENH.	-	-	-	5
Hantzschia amphioxys (EHR.) GRUN.	100	100	90	70
Navicula atomus (NÄG.) GRUN.	100	100	100	25
N. contenta GRUN.	-	-	85	10
N. cryptocephala KÜTZ.	-	-	-	5
N. mutica KÜTZ.	30	20	85	5
N. seminulum GRUN.	-	10	35	-
N. tantula HUSTEDT	40	35	100	-
Nitzschia acidoclinata LANGE-BERT.	45	70	95	-
N. inconspigua GRUN.	-	5	25	-
N. palea (KÜTZ.) W. SMITH	85	90	90	-
N. pusilla GRUN.	95	100	40	-
N. terrestris (BOYE-PET.) HUST.	-	-	60	-
Nitzschia sp.	-	-	-	5
Pinnularia borealis EHR.	40	90	50	-
P. microstauron (EHR.) CLEVE	-	-	15	-
P. obscura HUSTEDT	70	80	60	5
P. subcapitata GREG.	85	100	100	25
P. viridis var. *sudetica* (HILSE) HUST.	15	20	95	-
Stauroneis thermicola (BOYE-PET.) LUND	90	85	95	-
CHRYSOPHYCEAE				
stages similar to the g. *Chrysosphaera*	-	5	50	-
EUSTIGMATOPHYCEAE				
Eustigmatos magnus (BOYE-PET.) HIBBERD	100	95	100	80
Monodopsis subterranea (BOYE-PET.) HIBBERD	95	100	100	-
Vischeria helvetica (VISCH. et PASCH.) HIBBERD	50	55	75	35

Table 3. (continued)

	Fi	Fa	M	Fo
XANTHOPHYCEAE				
Botrydiopsis intercedens PASCH.	65	70	85	75
Bumilleriopsis terricola MATV.	15	15	-	-
Characiopsis sp.	15	40	-	25
Heterococcus sp.	35	15	50	45
Heterothrix bristoliana PASCH.	90	90	90	5
H. debilis VISCH.	100	100	100	45
H. monochloron var. *terrestris* ETTL et KÁCHA	-	-	10	-
H. montana VISCH.	30	-	-	-
CHLOROPHYCEAE				
Actinotaenium cucurbita (BRÉB.) TEIL.	-	5	5	-
Bracteacoccus minor (CHOD.) PETROVÁ	80	95	85	100
Chlamydomonas applanata PRINGSH.	-	10	40	-
Ch. augustae SKUJA	-	-	-	35
Ch. callunae ETTL	45	40	30	65
Ch. chlorostellata FLINT et ETTL	-	-	-	20
Ch. culleus ETTL	-	20	30	-
Ch. intermedia CHOD.	80	80	10	-
Ch. cf. *lobulata* ETTL	-	-	10	-
Ch. macrostellata LUND	15	25	30	60
Ch. moewusii GERL.	-	-	-	25
Ch. peterfii GERL.	85	70	75	-
Ch. pseudogleogama GERL.	35	25	30	-
Ch. raudensis ETTL	-	-	5	-
Ch. reisiglii ETTL	25	-	-	-
Ch. segnis ETTL	-	15	50	-
Ch. snowiae PRINTZ	95	80	15	-
Ch. subfusiformis GERL.	15	15	35	-
Ch. texensis KING	30	-	-	-
Ch. thomassonii ETTL	-	15	25	-
Chlamydomonas sp. div.	85	75	65	95
Chlamydopodium starrii (FOTT) ETTL et GÄRTNER	-	5	10	-
Chlorella ellipsoidea GERN.	90	85	95	90
Ch. homosphaera SKUJA	90	100	100	55
Ch. mirabilis ANDR.	60	75	70	-
Ch. vulgaris BEIJ.	100	100	80	45
Chlorella sp.	40	45	15	-
Chlorococcum cf. *compactum* ETTL et GÄRTNER	-	-	-	65
Ch. elkhartiense ARCH. et BOLD	65	60	80	35
Ch. infusionum (SCHRANK) MENEGH.	60	45	45	65
Ch. isabeliense ARCH. et BOLD	15	5	10	-
Ch. cf. *lobatum* (KORŠ.) FRITSCH et JOHN	-	10	30	35
Ch. oleofaciens TRAINOR et BOLD	50	45	55	40
Ch. robustum ETTL et GÄRTNER	20	15	25	-
Ch. schwarzii ETTL et GÄRTNER	-	-	60	65
Ch. sphacosum ARCH. et BOLD	10	-	-	-
Chlorococcum sp. 1	-	-	-	75
Chlorococcum sp. div.	75	90	50	40
Chloromonas rosae (ETTL H. et O.) ETTL.	-	-	15	75

Table 3. (continued)

	Fi	Fa	M	Fo
Chlorosarcinopsis sp.	15	20	15	-
Choricystis sp.	20	45	65	-
Coccomyxa gleobotrydiformis REISIGL	85	85	95	100
Coenochloris cf. *bilobata* (BROADY) HIND.	50	75	45	-
Cosmarium sp.	-	-	25	-
Cylindrocystis brebissonii MENEGH.	35	45	20	-
Dictyosphaerium chlorelloides (NAUM.) KOM. et PERM.	25	20	15	-
Diplosphaera chodati BIALOSUKNIA	15	55	30	70
Euastrum insulare (WITTR.) ROY	-	-	25	-
Fernandinella alpina CHOD.	50	30	30	-
Heterochlamydomonas lobata LANGFORD et COX	-	-	35	30
Keratococcus bicaudatus (A. BR.) BOYE-PET.	10	70	60	-
Klebsormidium flaccidum (KÜTZ.) SILVA, MATT. et BLACK.	100	100	75	100
Lobosphaera sp.	85	85	80	-
Mesotaenium endlicherianum NÄG.	-	25	35	-
Myrmecia bisecta REISIGL	15	30	90	65
Neochloris alveolaris BOLD	55	70	85	-
N. pseudoalveolaris DEAS. et BOLD	-	-	-	20
Neochlorosarcina minuta (GROOVER et BOLD) S. WATAN.	80	90	95	-
Planophila terrestris GROOVER et HOFST.	55	60	85	-
Pleurastrum sarcinoideum GROOVER et BOLD	100	80	100	-
Protosiphon botryoides (KÜTZ.) KLEBS	80	65	40	-
Pseudendoclonium basiliense VISCH.	10	5	-	-
Pseudococcomyxa simplex (MAINX) FOTT	95	95	100	70
Leptosira erumpens (DEAS. et BOLD) LUKEŠ.	30	30	30	-
Rhexinema paucicellulare (VISCH.) GEITL.	5	-	-	-
Scotiellopsis terrestris (REISIGL) PUNČ. et KAL.	100	100	100	45
S. cf. *rubescens* VINATZ.	70	70	85	-
Spongiochloris excentrica STARR	15	-	-	-
Spongiochloris sp.	-	5	75	80
Stichococcus bacillaris NÄG.	90	100	95	100
Tetracystis aggregata BROWN et BOLD	100	100	100	80
EUGLENOPHYCEAE				
Euglena sp.	25	15	-	-

The greatest species diversity was found in the meadow (99 species), followed by the fallow (90), the field (85) and the forest (49). The same trend was observed in numbers of highly constant species: meadow 41, fallow 34, field 32 and forest 12 species. However, many of highly constant algal species of all localities excepting forest appeared only in a very low abundance. There were, for example, *Klebsormidium flaccidum, Nostoc minutum, Heterothrix bristoliana* in the field, *Klebsormidium flaccidum, Pinnularia borealis, Eustigmatos magnus, Heterothrix bristoliana, Phormidium autumnale* in the fallow, and *Klebsormidium flaccidum, Phormidium autumnale* and *Leptolyngbya nostocorum* in the meadow.

27 species were recorded in all stages, 5 species (6 %) were unique to the field, 10 (10 %) to the meadow and 10 species (20 %) to the forest (see Table 3).

No prominent dominant species were discovered in the field, the fallow and the meadow. *Stichococcus bacillaris* and *Klebsormidium flaccidum* prevailed in forest litter. *Chlorococcum* and *Chlamydomonas* species were main dominants of forest soil.

As to the floristic similarity, the most similar algal community was found between the field and the fallow ($S_s = 0.8914$), and the similarity decreased in the sequence, fallow - meadow ($S_s = 0.8783$), field - meadow ($S_s = 0.7935$), meadow - forest ($S_s = 0.5000$), fallow - forest ($S_s = 0.4892$) and field - forest ($S_s = 0.4776$).

Three large groups of samples are distinguishable on the dendrogram of cluster analysis (Fig. 2). The first and largest group is formed by samples from the field and the fallow, the second one by samples from the meadow and the third one, most heterogenous, by samples from the forest. The separation of the forest from younger successional stages is visible already in the first level of dichotomic branching.

Vertical distribution

The litter and soil surface (0–1 cm) layer of all successional stages contained both quantitatively and qualitatively richer algal communities compared with the 1–10 cm layer (Tab. 2, Fig. 1). The most significant decline in algal quantity with soil depth was recovered in the fallow (only 6 % of surface counts), the lowest one in the meadow (37.5 % of surface counts). As concerns individual algal groups, counts of Bacillariophyceae decreased usually most remarkably, especially in the field and the meadow (Tab. 2).

The decrease of algal species diversity with soil depth was found less prominent, being significant only in the fallow and the meadow (Fig. 1).

The fallow was chosen for a more detailed demonstration of the vertical distribution of algae to the depth of 52 cm. The most distinct drop of algal counts was observed immediately below the upper 0–2 cm soil layer (Tab. 4). Then, algal counts decreased more gently and continuously down to the depth of 25–26 cm (to the weathering bedrock respectively) and deeper they were hardly detectable. On the contrary, the decrease of algal species diversity was not so regular and so remarkable, still reaching 23 species in the depth below 50 cm (Tab. 4).

Horizontal distribution

In view of species composition, the algal communities of the fallow and the meadow with about 60 % of highly frequent species appeared the most homogeneous, whereas that of the forest with only 25 % of highly frequent and more than 60 % of lowly frequent species was considered to be the most heterogenous (Tab. 5).

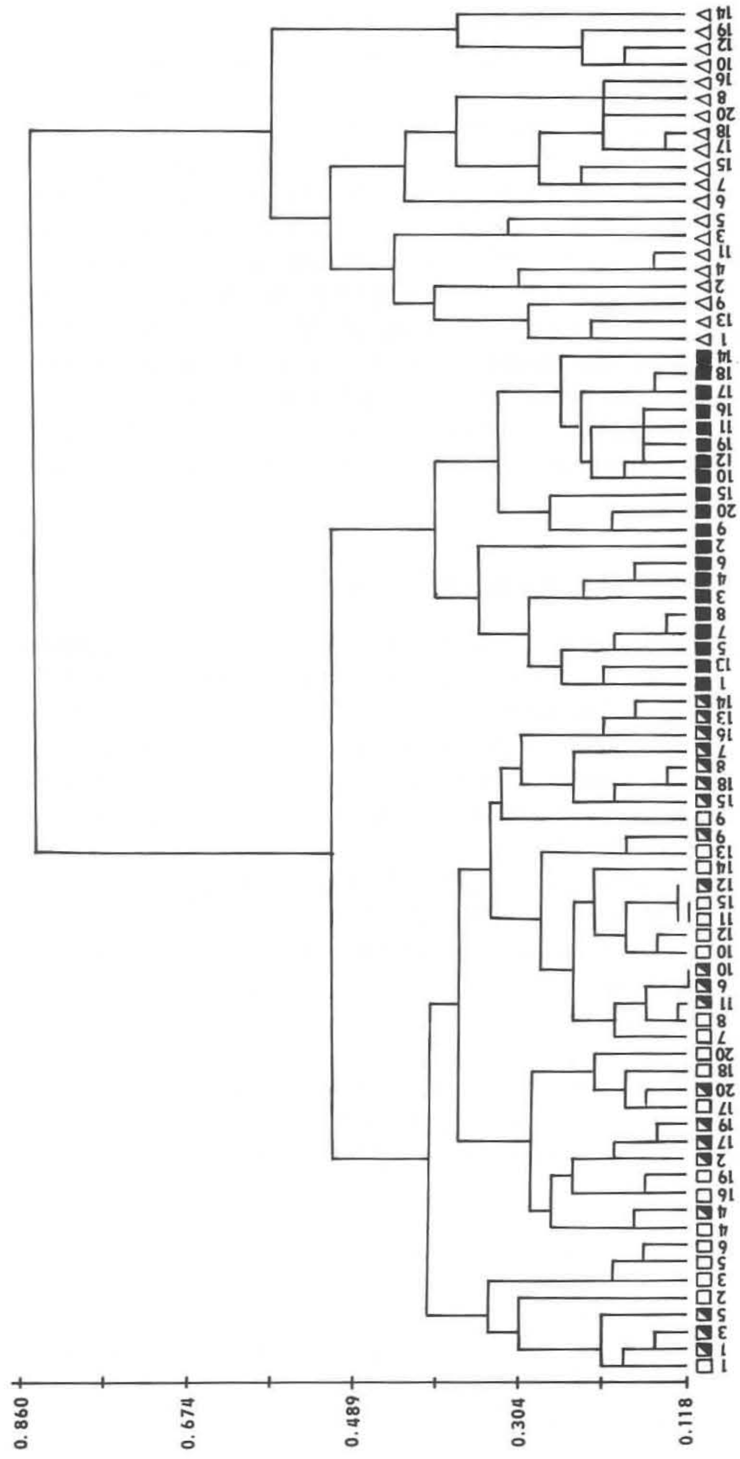

Fig. 2. Dendrogram of cluster analysis. □ field, ◪ fallow, ■ meadow, △ forest; 1–20 . . . numbers of soil samples corresponding to individual consecutive sampling occasions.

Table 4. Numbers ($\cdot 10^3 \cdot g^{-1}$ d · w · of soil) and species diversity of algae in the fallow soil profile (13. 11. 1989).

Algal group / Depth [cm]	CH + X + E	C	B	Total	Number of species
0–2	697	57	1.1	755.1	40
10–12	94	3	< 0.1	97.0	30
20–22	79	3	0.1	82.0	35
25–26	65	< 0.1	< 0.1	65.0	24
30–32	2	< 0.1	0.1	2.0	19
40–42	2	0.1	0.3	2.4	28
50–52	1	< 0.1	0.1	1.1	23

As concerns algal counts from the main systematic groups, big differences in coefficient of variation were found between both sampling occasions (see Table 6). Generally, the horizontal distribution of the CH + X + E counts seemed to be more homogenous (V = 24–47 %) than that of Bacillariophyceae and Cyanophyceae (V = up to 129 %). The greatest horizontal CH + X + E heterogeneity was revealed in the forest, the greatest heterogeneity of Bacillariophyceae in the field and that of Cyanophyceae in the fallow (Tab. 6).

Seasonal changes

As evident from Figure 3, peaks of algal abundance occurred usually in the spring and autumn seasons. Shifts of maxima were observed, probably in dependence on climatic conditions of individual years and on successional stages.

The temporal changes of algal counts of all main groups were usually more distinct in the upper 0–1 cm soil layers in comparison with the deeper ones. The greatest variations in algal counts were found in the forest and in the field.

Table 5. Heterogeneity of algal species composition in surface (0–1 cm) soil layer. Percentage proportion of species with low and high frequency (n = 5) on first (a) and second (b) sampling occasion.

Frequency	Field		Fallow		Meadow		Forest	
	a	b	a	b	a	b	a	b
High	44	37	67	58	53	60	24	27
Low	42	48	21	24	32	27	60	65

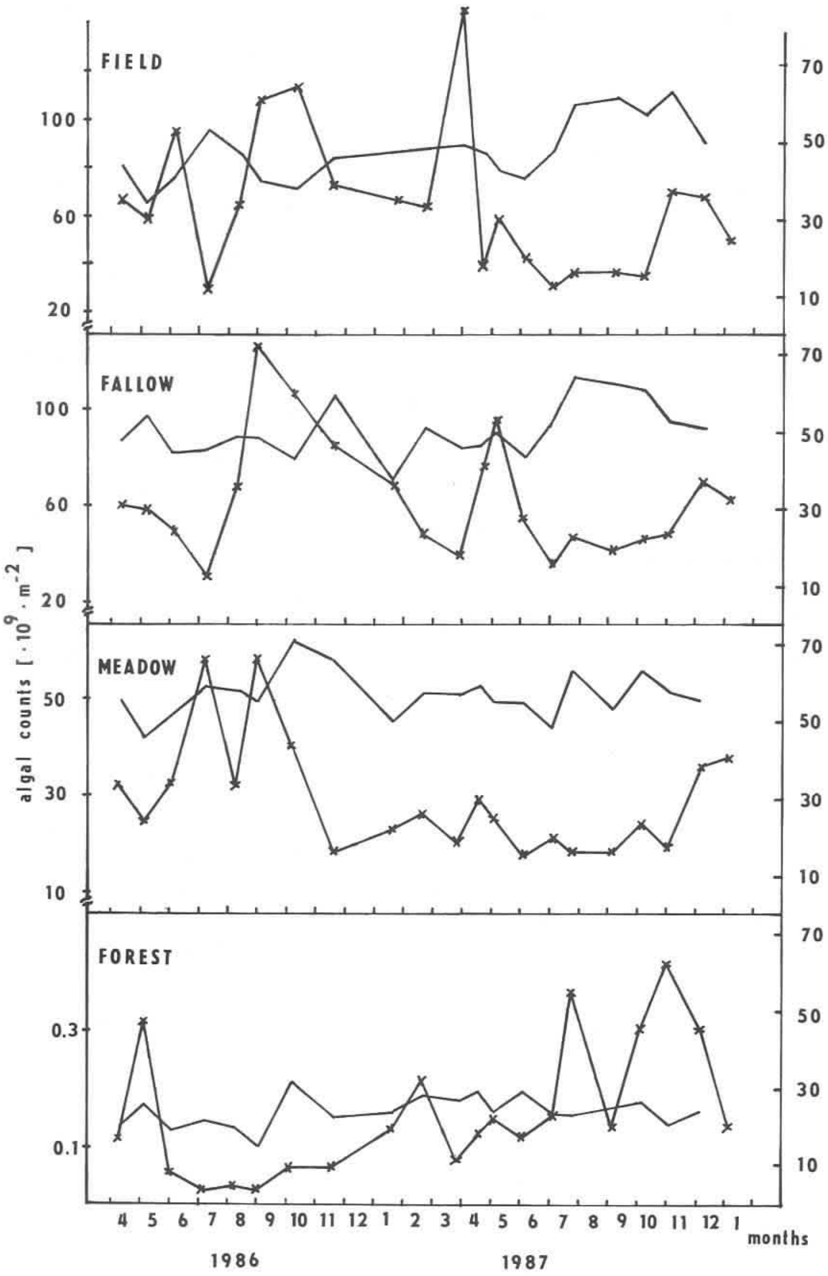

Fig. 3. Temporal changes of algal cell counts [$\cdot 10^9 \cdot m^{-2}$] and of algal species numbers in 0–10 cm soil layer. x——x algal counts, —— number of species.

Table 6. Heterogeneity of algal numbers in the surface (0–1 cm) soil layer. Coefficient of variance (V [%], n = 5) on first (a) and second (b) sampling occasion.

Algal group	Field		Fallow		Meadow		Forest	
	a	b	a	b	a	b	a	b
CH + X + E	41	24	28	28	35	33	34	47
Bacillariophyceae	80	110	129	35	87	70	–	–
Cyanophyceae	41	39	128	56	32	63	–	–

Bacillariophyceae and Cyanophyceae varied more remarkably than CH + X + E (Tab. 2).

The changes in algae species diversity were little prominent, coefficients of variation ranging between 10,4 % (meadow) and 16,8 % (fallow).

No correlation between the quantity of algae and soil moisture was determined. The effect of temperature (negative correlation with counts of Bacillariophyceae and positive correlation with those of Cyanophyceae at ($\alpha = 0.05$) was found in some cases only.

Ordination analysis

The ordination analysis of samples (Fig. 4) confirmed the results obtained by both coenological and cluster analyses and indicated the relationships of algal communities of successional stages studied. The first axis (I) can be interpreted as a successional gradient.

It is possible to distinquish three separated areas: the first one on the axis I (in left-right direction) consists of mixed samples from the field and the fallow, which indicates close similarity of algal communities of both localities. The second area, occurring very near the first one, consists of soil meadow samples. Relatively small size of both areas indicates large homogeneity of the samples from younger successional stages. The third area, being in a great distance from two previous, represents the forest samples; its large size is due to a great variability of samples connected probably with the great spatial heterogeneity of algal community in the forest (Tabs 5, 6). This big distance between mentioned areas reflects great difference in their successional age and a more different ecological situation in the forest as compared with the field – fallow – meadow complex.

No shifts in the direction of axis I, i. e., no one-way changes of algal communities of individual successional stages were found during the time of investigation, and all changes observed are to be interpreted as fluctuations.

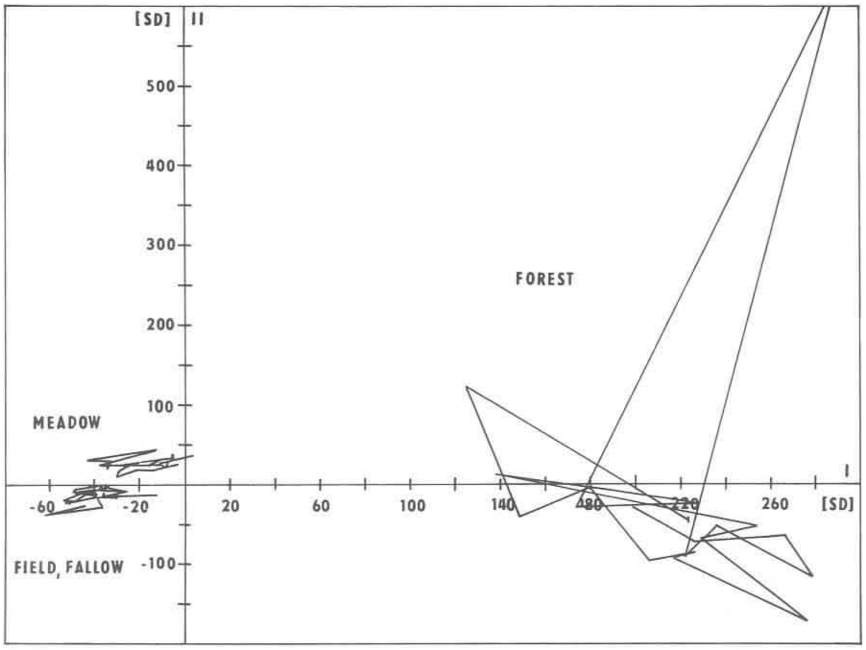

Fig. 4. Ordination of samples; axes I and II were used for depicting.

Discussion

The comparability of our results with literary data is limited for following reasons: 1) quantitative and qualitative methods, soil sampling, duration of investigation, as well as character of studied ecosystems, are mostly different; 2) numerous phycologists identify algae to the generic level only.

The great algal species diversity and the prevalence of Chlorophyceae were characteristic for the area studied. Literary data from the same soil type are absent, however, great similarity could be found with algal communities of podzols or brown podzolized soils (ŠTINA 1959, POCIENE 1967).

The dominance of Chlorophyceae is probably connected with a rather low pH of the studied soils that usually supports intensive development and diversity of green algae in different biotopes (MAC ENTEE et al. 1972, MAC ENTEE & BOLD 1974, NAKANO 1981 etc.).

The explanation of a greater species diversity on our localities than that on the analogous ones, given in literature, could be due to the fact that a correct species identification within some genera is very complicated and time-consuming, and therefore often "complexes" of species, (for example *Chlorococcum humicola;* ETTL & GÄRTNER 1990), appear in lists of soil algae under one and the same name.

The majority of species found simultaneously in four or, at least, in three successional stages studied by us, e. g., *Phormidium autumnale, Navicula mutica, Hantzschia amphioxys, Monodopsis subterranea, Klebsormidium flaccidum, Stichococcus bacillaris* are cosmopolitan species, widespread in different soils. Some others, namely *Neochlorosarcina minuta, Tetracystis aggregata, Chlorella mirabilis, Leptosira erumpens, Pleurastrum sarcinoideum,* are very scarcely mentioned in literature and little known, so that it is not possible to make any conclusions about their geographic distribution and autecology.

Species occurring in one or two of our localities only possibly require more specific conditions. The occurrence of hygrophilous species in the meadow, (e. g., *Microchaete tenera, Euastrum insulare,* hygrophilous diatoms and *Chlamydomonas* spp.), reflects high soil moisture of this locality. The maximal occurrence of *Chlamydomonas augustae, C. chlorostellata* and *Chloromonas rosae* in the forest studied is in agreement with literature and confirms a close relation of these species to forest soils.

Biological, ecological and systematic notes about the less known or interesting species found in studied successional stages will be published separately.

Soil algal communities of individual successional stages differed more or less in all characteristics studied, i. e. in algal counts, species composition, spatial distribution and seasonal dynamics.

Significantly higher counts and species diversity of algae in young successional stages (i. e. field, fallow and meadow) compared with the forest are in agreement with the results of many algologists studying arable, or otherwise disturbed soils, together with the forest ones (ŠTINA 1959, MAC ENTEE 1970, SUDAKOVA 1977, NAKANO 1981 etc.). In young stages, algal counts were comparable with those of actinomycetes, lower on two orders than the counts of bacteria and higher on one order than the counts of micromycetes. In the forest, quantity of algae was much lower than that of other microorganisms (KRIŠTŮFEK, ŘEPOVÁ, ŠANTRŮČKOVÁ, pers. comm.). Both qualitatively and quantitatively poor forest algal community was probably result of less favourable soil pH, especially for cyanobacteria (ARCHIBALD 1972, KING & WARD 1977, NOSKOVA 1977, CARSON & BROWN 1978, ZIMMERMAN et al. 1980, etc.), of limited light input (SHIMMEL & DARLEY 1985, MARKOVA 1974, ŠUŠUJEVA 1977, ŠALAR' 1986, etc.), of lower nutrients content (JOHNSON 1974), of litter character (HOLLERBACH & ŠTINA 1969) and of higher content of organic matter (NAKANO 1981). In agreement with the results of NAKANO (1981), an opposite trend of organic matter content (C_{org} [%]) and algal counts was observed in localities studied (compare Tabs 1, 2).

The establishment of a forest ecosystem was found as the crucial point for changes in species composition of algae also during primary succession on inland sand dunes of The Netherlands (LUKEŠOVÁ, in prep.).

A greater algal species diversity in the meadow than in the fallow and the field was due to the presence of many hygrophilous species caused by a high soil moisture content of this locality.

Our results can be compared with the data published by HUNT et al. (1979) concerning 1 and 11 years old fields and a 250 years old climax forest. The same trend in algal and cyanobacterial counts (their decrease with the age of successional stage), the same dominant group and the same ranges of algal counts were found in both cases, despite a different soil type, climatic region and methods used. Some differences in the trend of algal diversity could be explained, for example, through the identification of algae by mentioned authors only up to the generic level.

The greatest horizontal heterogeneity of the algal community in the forest soil was probably connected with the heterogeneity of plant cover (ALEKSACHINA & ŠTINA 1984) and consequently with various microhabitats differing by light input, moisture, litter amount, nutrients content etc.

A greater heterogeneity of Bacillariophyceae and Cyanophyceae than that of Chlorophyceae observed in the studied localities is in agreement with literary data (NĚKRASOVA & BUSYGINA 1979, DOMRAČEVA 1977); according to them, it could be connected with biological peculiarities of algae, especially with the character of their reproduction. → zoospores in Chlorophyceae only

Algae as photoautotrophs reach the maximum of their development in the upper soil layers (except after heavy rainfall, ploughing, etc.). The decrease of algal quantity and species diversity with soil depth, the intensity of which varies according to type of biotope, is a regular phenomenon (ŠTINA & HOLLERBACH 1976, ALEKSACHINA & ŠTINA 1984, etc.). The significant decrease of algal diversity with soil depth in the fallow and meadow was probably caused by the greater proportion of aerophytic species the development of which is favoured in nondisturbed (for example by agricultural practice) top soil layers.

Unlike a prominent decrease of algal diversity, a relatively low drop of algal counts with soil depth was observed in the meadow. This can be explained by a greater density and depth of plant roots, by a rather high soil moisture and finally by a greater abundance and activity of soil animals. The last presumption seems to be confirmed by gut contents and faeces analysis of soil animals collected from this locality. The gut contents as well as animal feaces, especially of earthworms, were rich in viable algae (LUKEŠOVÁ, unpublished data) which can be spread by migration of animals through the soil profile.

Despite the most intensive decrease of algal quantity below the upper layer of 0–2 cm, still high values of algal counts were recorded below the depth of 20 cm (Tab. 4). The majority of algal species isolated from deeper layers, out of the reach of light penetration, do not form any akinetes, zygotes or other resting stages. Probably the ability of many soil algae to replace the phototrophic way of life by the heterotrophic one, as was demonstrated in laboratory experiments many times (data reviewed by METTING 1981), could help algae to survive and to live successfully in deeper soil layers. However, the situation in natural soil conditions is quite unknown and needs a detailed investigation.

Unlike water biotopes, where seasonal changes of dominants are a regular phenomenon, any similar trend was neither found in our soils nor is known from literature (LUND 1945, 1962, ŠUŠUJEVA 1984, etc.). It could be caused by the use of various, usually indirect, cultivation qualitative methods, or by a great resistance of soil algae to the influence of unfavourable ecological conditions. Only in some cases, a reduced species composition (disappearance of nonresistant species) was observed during summer season in hot and dry regions (MARKOVA 1974, NOVIČKOVA-IVANOVA & ČAPLYGINA 1979).

Despite different quantitative methods, the great fluctuation of algal counts in studied ecosystems corresponds with data both from analogous and from various other biotopes (HUNT et al. 1979, RUBBLE & DAVIS 1988). The wide range of algal counts fluctuation in studied field was probably caused by farming practices, in the forest due to heterogeneity of this locality.

A greater temporal fluctuation of algal counts in the upper soil layers than in the deeper ones was connected probably with a greater variability of abiotic factors, e.g., of moisture (Tab. 1), temperature, light input, etc.

Although soil moisture is usually reported as a factor regulating seasonal changes of soil algae quantity, this effect was not registered in the studied localities. The possible explanation is that soil moisture (40–60 %WHC in average) did not sink below 10 % WHC on any sampling occasion and was no limiting factor. Month intervals between sampling occasions are probably too long (DOMRAČEVA 1974, PERMINOVA 1980) and therefore unsufficient for a correct evaluation of relationships between algal counts and soil moisture.

Farming practices could be the main factor affecting temporal fluctuation of algal quantity in the field (survey in HOLLERBACH & ŠTINA 1969). For example, the decrease of algal counts was observed after the treatment with herbicides or after ploughing (in the upper soil layer); on the contrary, the increase of algal counts was recorded after application of mineral fertilizers.

Soil animals probably play an important role in the regulation of algae in the meadow and the forest where high abundance of soil animals was found (personal comm. of zoologists participating in this project). This presumption is supported by literature (DOMRAČEVA 1974), as well as by the results from food-preferential experiments and gut contents and faeces analyses of soil animals collected in studied localities (LUKEŠOVÁ, in prep.).

No successional changes of algal communities were observed during the two-years investigation either in the fallow or in other successional stages. During this period, algal communities of the fallow and the field were closely related one to another (Fig. 4). During less intensive studies in 1988–1990, some changes in species composition were found in the field, namely the occurrence of new, previously not recorded species of Chlorophyceae (*Actinochloris terrestris, Raphidonema* sp.) and Cyanophyceae (*Nostoc edaphicum, Nostoc* sp., *Scytonema hoffmanii*).

As follows from presented results, crop rotation was more important for affecting the composition of the algal community than continuous changes connected with the secondary succession.

The gradual decrease of mean total algal counts during the succession, probably as a result of increasing plant cover density, indicates that quantitative changes precede the qualitative ones during the secondary succession.

Acknowledgements

This work was supported by the Institute of Soil Biology, Czechoslovak Academy of Sciences, as a part of the project "Biological structure and function of the soil part of ecosystems". I thank Dr. HANUŠ ETTL for his kind help with the identification of some *Chlorococcum* and *Chlamydomonas* spp. I would like also to thank Dr. MARTA TESAŘOVÁ for critical revision of the manuscript and Mr. J. KALČÍK and Dr. K. MATĚJKA for kindly providing P_{tot} and plant biomass data.

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Manuscript received November, 25, 1992, accepted March, 31, 1993.

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